Distinguishing forest tree communities in Kibale National Park, western Uganda using ordination and classification methods

Patrick Mucunguzi[1,*], John Kasenene[1], Jeremy Midgley[2], Paul Ssegawa[1] and John R. S. Tabuti[1]

[1]*Department of Botany, Makerere University, PO Box 7062, Kampala, Uganda and* [2]*Department of Botany, University of Cape Town, Private Bag X3, Rondesbosch 7701, South Africa*

Abstract

A study of spatial variation in tree community structure and species composition in the Kibale National Park, western Uganda was conducted. Tree communities were compared at five sites namely K-14, K-15 and K-30 at Kanyawara in the north, Ngogo in the central part of the forest and Mainaro in the southern part. All trees ≥10-cm diameter at breast height were censused along belt transects covering a total of 15 ha in all sites. Cluster analysis and principal component analysis were used to identify forest tree communities and species associations. Using cluster analysis, two species assemblages emerged: the Mainaro, Ngogo and K-15 cluster and the K-30 and K-14 cluster. Principal component analysis revealed the descriptive species for the northern and southern sites.

Key words: ordination, species associations, tree community

Introduction

Trees are responsible for much of the biomass in tropical forest ecosystems. Their distribution and abundance strongly influences the abundance of other organisms in these ecosystems (Davies, 1994; Hart, 2001; Brugiere *et al.*, 2002). Many studies of tree community structure and species composition conducted throughout the tropics indicate that tropical forest tree community structure and species composition varies widely between forests in different continents (Phillips *et al.*, 1994), on the same continent (Ter Steege *et al.*, 2000) and different sites within the same forest (Proctor *et al.*, 1983).

Most studies of intra forest variation in tree structure and composition have compared sites that differ in forest type (e.g. lowland versus montane, undisturbed versus disturbed). It is therefore not entirely surprising that the identities and densities of tree species generally differ markedly between sites in these studies (Parthasarathy, 1999; Swamy *et al.*, 2000). Comparisons between sites ≥5 km apart of similar forest types within the same forest have been less common (Butynski, 1990; Chapman *et al.*, 1997). Nevertheless, studies conducted in the Kibale forest, Uganda suggest that even within the same forest type, considerable spatial heterogeneity in tree community structure and composition can exist (Butynski, 1990; Chapman *et al.*, 1997).

Traditional approaches to investigate plant communities often use ordination and classification methods (Okland, 1990; Kent & Coker, 1992). These include direct and indirect gradient analysis techniques (Jongman, Ter Braak & Van Tongeren, 1995). Indirect gradient techniques of data analysis such as principal Components Analysis (PCA) and cluster analysis (CA) provide means of generating and evaluating a classification of plant communities and enable the detection of patterns (Okland, 1990; Jongman *et al.*, 1995). Such methods work best when environmental data are collected to determine factors affecting species composition.

Although there have been studies carried out in Kibale National Park by Butynski (1990) and Chapman *et al.* (1997) to identify the various vegetation types, the methods and approaches used were different. The aim of

*Correspondence: E-mail: pmucunguzi@botany.mak.ac.ug

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this study was to determine the tree communities in different predetermined forest types, to establish the degree of similarity between sites, and the different tree species associations. The most widespread and restricted tree species were also identified. We predicted that sites which experienced similar management regimes in the past will tend to have similar species assemblages and would be reflected in the species associations.

Materials and methods

Study area

Kibale National Park includes a medium altitude (1110–1590 m above sea level.) transitional, moist forest interposed between dry tropical and wet tropical rain forest in the Albertine region (0°13′–41′N and 30°19′–30°32′E) in western Uganda (Howard & Davenport, 1996; Struhsaker, 1997). The protected area, which covers 766 km^2, was declared a National Park in 1993. Kibale forest covers numerous hills, valleys, swamps and streams. The rainfall ranges from 1490 mm at Ngogo to 1622 mm at Kanyawara and distributed in two wetter seasons that include March–May and September–November (Struhsaker, 1997). Mean annual temperature of the reserve is 20.5°C and varies little during the year.

This study was carried out in five study sites namely K-15, K-14 and K-30 at Kanyawara, Ngogo and Mainaro. These sites were at different locations of the forest (north, central and south) and had differences in dominant species and levels of anthropogenic disturbances (Table 1; Ghiglieri, 1984; Howard, 1991; Kasenene, 1987; Osmaston, 1959; Skorupa & Kasenene, 1984; Skorupa, 1988; Van Orsdol, 1983).

Table 1 Characteristics of the study sites

Study sites	Location	Dominant species	Level of disturbance
K-15 (Kanyawara)	North	*Parinari excelsa*	Heavily logged
K-14 (Kanyawara)	North	*Parinari excelsa*	Moderately logged
K-30 (Kanyawara)	North	*Parinari excelsa*	Unlogged
Ngogo	Central	*Pterygota mildbraedii*	Unlogged
Mainaro	South	*Cynometra alexandri*	Heavily logged and encroached

Floristic composition assessment

The stratified random sampling technique based on forest types and intensity of logging, with completely random samples in each of the strata was used to locate the sampling plots (n = 150). Within each forest type, a sample of 30 of 0.1 ha (10 × 100 m) belt transects were randomly established. The belt transects were oriented to run across similar topographical gradient of valley, lower slope, and upper slope to cover identical vegetation in all study areas. All trees ≥10-cm diameter at breast height (dbh) were enumerated and identified to species level. Species nomenclature is a according to Polhill *et al.* (1952).

Data analysis

Data for this study was analysed using CA and principal component analysis. CA is a technique that sorts objects (such as sampling units) into groups or clusters based upon their overall resemblance to one another (Ludwig & Reynolds, 1988). PCA is an ordination technique (Pielou, 1984) which partitions a resemblance matrix (variance–covariance or correlation) into a set of orthogonal (perpendicular) axes or PCA 'components' (Ludwig & Reynolds, 1988). The first few PCA components will explain the largest percentage of variation in the data set (Gauch, 1982) and ordinations of sampling units on these axes provide information about the ecological relationship between them. Differences in species richness between forest types were analysed using the chi-squared technique at a level of significance of 95%.

Tree community structure analysis

The presence of 113 tree species was recorded in binary (presence or absence) format for each of the five sites studied. A matrix of species by study sites was arranged to determine similarity of sites in terms of species assemblage. A Jaccard's Index (JI) was calculated (Ludwig & Reynolds, 1988). JI is expressed as:

$$\mathrm{JI} = a/(a + b + c),$$

where a is the number of species that sites A and B have in common, b as the number of species present in site A but absent from site B and c as the number of species present in site B but absent from site A.

The JI ranges from near 0 (for sites highly dissimilar with respect to species) to near 1 (for sites that are very

similar). An agglomerative clustering technique (weighted centroid) provided in the Multivariate Statistical Package (MVSP) of Kovach (1999) was used to produce a dendrogram containing all five sites. A minimum JI of 0.0 was used for defining clusters. Several algorithms were explored and clusters determined from one of the CA methods based on the underlying 'ecological knowledge of the data' (Ludwig & Reynolds, 1988). Other measures of similarity and measures of distance between sites were explored along with several different methods of clustering. All techniques provided similar results, with the JI and weighted centroid clustering being most meaningful ecologically.

Species associations

The two groups of sites produced by CA were considered unique for the analysis of species associations. From the absence–presence data from sampled sites, two new arrays were created based on site clusters A and B. Each array contained binary information for species present in more than 4% of quadrats sampled in sites of its corresponding cluster. The species which occurred in <4% of the quadrats sampled were considered rare and were removed from the data set to avoid introducing unnecessary noise (Mentis, 1983). This is justified for two reasons. First, the occurrences of rare species are usually more a matter of chance than an indication of ecological condition. Secondly, most multivariate techniques are affected very little by rare species carrying such a small percentage of the overall information of variance (Gauch, 1982). The two matrices produced were of sizes 90×69 (cluster A) and 60×103 (cluster B) where the rows represented the sampling quadrats and the columns the species. To determine any degree of similarity between species, the two arrays were used separately to calculate simple matching coefficients (SM) of Kovach (1999), for each species pair (A and B) using the following expression:

$$\mathrm{SM} = (\mathrm{a} + \mathrm{d})/(\mathrm{a} + \mathrm{b} + \mathrm{c} + \mathrm{d}),$$

whereby *a* is the number of quadrats containing species A and B; *b* the number of quadrats where species A was present but species B was absent; *c* the number of quadrats where species B was present but species A was absent; *d* the number of quadrats where neither species A or B were present. The SM ranges from 0 to 1. Species which rarely occur together would have a coefficient of 0, while those which normally occur together would have a coefficient of 1.

Two separate weighted centroid cluster analyses were conducted to produce dendrograms using MVSP (Kovach, 1999). By this analysis, tree species were grouped according to their frequency of occurrence in the study sites. A minimum SM of 0.0 was used to define species assemblages. As with the CA of the sites, other measures of similarity among species were attempted along with several different methods of clustering. All techniques provided similar results, with the SM and weighted centroid clustering making the most sense ecologically.

Results

Sites similarity

The study recorded 67, 66, 59, 61 and 54 tree species for Kanyawara K-30, K-14 and K-15, Ngogo and Mainaro respectively. There was no significant difference in the species richness in the five forest types despite the tendency of disturbed forests to have fewer species (χ^2, $P > 0.05$).

Cluster analysis produced two distinct groups, clusters A and B. Cluster A included Mainoro, Ngogo and Kanyawara K-15 (Fig. 1). Cluster B included Kanyawara K-14 and K-30. The first two principal components (PC 1 and PC 2) from the PCA accounted for 67% of variance in binary species data (Table 2). The decomposition of the principal components provided insight into which species were responsible for defining the groups (Table 3). Species with relatively high loadings >0.062 on PC 1 are shown in Table 3 in bold. These species were descriptive of sites

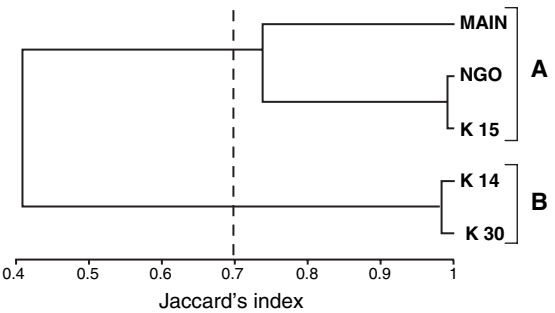

Fig 1 Cluster analysis of five sites in Kibale forest based upon presence or absence of 113 naturally occurring tree species. The letters (A and B) indicate clusters defined by using a minimum Jaccard's Index of 0.7 (dashed line)

Table 2 Scores of the five sites on principal components axes 1 and 2 (PC 1 and PC 2) and percent of total variance in species richness explained by each PC axis

Sites	PC I	PC 2
K-30	0.567	−0.073
K-14	0.57	−0.101
K-15	0.371	−0.021
Ngogo	0.45	−0.026
Mainaro	0.12	0.992
% of total variance (cumulative in parentheses)	47.4 (47.4)	19.9 (67.3)

Kanyawara K-30 and K-14. There were no sites with negative scores on PC 1 (Table 2). Species with relatively high negative scores on PC 1 are shown in Table 3 but were not descriptive of any site as there were no sites with negative scores on PC 1 (Table 2).

Species with loadings >0.062 on PC 2 were descriptive of Mainaro, a member of cluster A (Fig. 1). Kanywara K-14 had a relatively high negative score on PC 2 (Table 2) although there were no species with loadings >0.062 on PC 2 (Table 3). Friedman test revealed a significant difference between clusters A and B on the basis of tree species (χ^2, $P < 0.05$).

Species associations

The two site clusters produced by CA were used to categorize tree species into assemblages which represented common associations of species found in the sites of each cluster. Sixty-nine species occurred at more than 4% of 90 sampling quadrats in sites of cluster A. Species paired by CA which had simple matching coefficient >0.9 are shown in Table 4. Four species assemblages were produced by CA for the sites in cluster A (Fig. 1; Table 5). The first species assemblage A1, had species common in the heavily logged Kanyawara K-15. The second assemblage A2, had common and some species restricted at Mainaro study site only (*Baphiopsis parviflora*, *Celtis mildbraedii* and *Phyllanthus discoideus*). The third assemblage, A3, had species common in the unlogged forest types at Ngogo and Kanyawara K-30 and the lightly logged forest Kanyawara K-14. The fourth assemblage, A4, had more species than A1–A3 combined. It was characterized by species common in Ngogo, Mainaro and the heavily logged Kanyawara K-15: *Piptadeniastrum africanum, Bequaertiodendron oblanceolata, Warburgia ugandensis* and *Harrisonia abyssinica* were mainly at Ngogo site. *Olea welwitschii, Kigelia moosa* and *Myrianthus arboreus* were common in the K-15 site.

One hundred and three species occurred at more than 4% of 60 sampling quadrats in cluster B. Species paired by CA which had a SM >0.9 are shown in Table 4. Four species assemblages were produced. Species assemblages B1 and B2 had species common in the unlogged K-30 and the lightly logged K-14 sites at Kanyawara with the exception of *Uvariopsis congensis* which was more common at Mainaro than Kanyawara. Assemblage B3 had many species common in both unlogged K-30 and Ngogo sites, while assemblage B4 had many species common to both Ngogo and Mainaro sites and rare at K-30 site.

Discussion

Similarity of sites

This study has improved the tree species inventory over previous lists. Struhsaker (1997) reported 51 species for K-30, -23, -18, and 52 for K-14, K-15 and Ngogo respectively. Chapman & Chapman (1997) recorded 88 and 29 species for Ngogo and Mainaro respectively. The lack of significant difference in species richness between logged and unlogged forest types indicates forest recovery after 28 years of postlogging. The findings agree with those of Cannon, Peart & Leighton (1998). This species richness of the logged forest is due to the recruitment of secondary colonizers. It may not indicate recovery to the original forest state.

The relatively undisturbed forest at Ngogo and the heavily disturbed forest of K-15 had similar floristic composition. This is possibly due to both forests being mixed forests characteristic of the central block. Heavy logging in K-15 resulted into growth of the secondary forest characterized mainly by *Celtis–Diospyros–Markhamia–Strombosia–Newtonia* mixed forest (Eilu, Hafashimana & Kasenene, 2004). Sheil, Sayer & Obrien (1999) noted that logging increases heterogeneity of the forest microhabitats and provides considerable space for colonization by good dispersers and disturbance dependent species. The descriptive species typical of cluster A (Table 3) are more abundant in areas that experienced logging.

Cluster B had the lightly logged forest (K-14) with the same number and type of tree species as the unlogged (K-30) forest. This indicates that the impact of logging on floristic composition appears to be dependent on the intensity of logging. These sites experienced lower effects of

Table 3 Loadings (correlations) of the original variables (species) on principal component axes 1 (PC I) and 2 (PC 2) for the five sites in Kibale forest

Species	PC 1	PC 2	Species	PC I	PC 2
Aningeria altissima	**0.096**	0.041	*Irvingia gabonensis*	0.008	−0.048
Aphania senegalensis	**0.096**	0.041	*Newtonia buchananii*	0.008	−0.048
Blighia welwitschii	**0.096**	0.041	*Oncoba routledge*	0.008	−0.048
Celtis africana	**0.096**	0.041	*Strychnos mitis*	0.008	−0.048
Celtis durandii	**0.096**	0.041	*Symphonia globulifera*	0.008	−0.048
Chaetachme aristata	**0.096**	0.041	*Albizia glaberrima*	0.008	0.05
Diospyros abyssinica	**0.096**	0.041	*Zanthoxylum leprieurii*	0	0.05
Dombeya mukole	**0.096**	0.041	*Alangium chinense*	−0.003	−0.044
Fagaropsis angolensis	**0.096**	0.041	*Schrebera arborea*	−0.003	−0.044
Funtumia latifolia	**0.096**	0.041	*Ehretia cymosa*	−0.011	−0.043
Markhamia lutea	**0.096**	0.041	*Bersama abyssinica*	−0.022	−0.036
Monodora myristica	**0.096**	0.041	*Hallea rubrostipulata*	−0.022	−0.036
Premna angolensis	**0.096**	0.041	*Tarenna pavetoides*	−0.046	−0.041
Prunus africana	**0.096**	0.041	*Clausena anisata*	−0.046	0.059
Trema orientalis	**0.096**	0.041	*Piptadeniastrum africanum*	−0.046	0.059
Trilepisium madagascariensis	**0.096**	0.041	*Pseudospondias microcarpa*	−0.046	0.059
Uvariopsis congensis	**0.096**	0.041	*Bridelia micrantha*	−0.053	0.06
Bombax buonopozense	**0.085**	−0.053	*Warburgia ugandensis*	−0.053	0.06
Cassipourea ruwensorensis	**0.085**	−0.053	*Erythrina excelsa*	−0.057	−0.034
Craterispermum laurinum	**0.085**	−0.053	*Pterygota mildbraedii*	−0.057	−0.034
Ilex mitis	**0.085**	−0.053	*Rauvolfia vomitaria*	−0.057	−0.034
Neoboutonia melleri	**0.085**	−0.053	*Syzygium guineense*	−0.057	−0.034
Olea welwitschii	**0.085**	−0.053	*Vangueria apiculata*	−0.057	−0.034
Parinari excelsa	**0.085**	−0.053	*Chionanthus mildbraedii*	−0.065	−0.034
Strombosia scheffleri	**0.085**	−0.053	*Majidea fosteri*	−0.065	−0.034
Tabernaemontana pachysiphon	**0.085**	−0.053	*Sapium ellipticum*	−0.065	−0.034
Dasylepis eggelingii	0.061	0.043	*Strombosiopsis tetrandra*	−0.065	−0.034
Dictyandra arborescens	0.061	0.043	*Baphiopsis parviflora*	−0.088	**0.062**
Ficus exasperata	0.061	0.043	*Bequaertiodendron oblanceolatum*	−0.088	**0.062**
Milletia dura	0.061	0.043	*Celtis mildbraedii*	−0.088	**0.062**
Polyscias fulva	0.061	0.043	*Celtis zenkeri*	−0.088	**0.062**
Spathodea campanulata	0.061	0.043	*Chrysophyllum albidum*	−0.088	**0.062**
Ficus sansibarica	0.054	0.043	*Cussonia holsti*	−0.088	**0.062**
Balanites wilsoniana	0.05	−0.051	*Cynometra alexandri*	−0.088	**0.062**
Chrysophyllum gorungosanum	0.05	−0.051	*Elaeophorbia* sp	−0.088	**0.062**
Coffea canephora	0.05	−0.051	*Ficus conraui*	−0.088	**0.062**
Cordia millenii	0.05	−0.051	*Ficus mucuso*	−0.088	**0.062**
Leptonychia mildbraedii	0.05	−0.051	*Glyphaea brevis*	−0.088	**0.062**
Lovoa swynnertonnii	0.05	−0.051	*Harrisonia abyssinica*	−0.088	**0.062**
Mimusops bagshawei	0.05	−0.051	*Lepidotrichilia volkensii*	−0.088	**0.062**
Myrianthus arboreus	0.043	−0.05	*Trichilia* sp1	−0.088	**0.062**
Rubiaceae	0.043	−0.05	*Albizia gummifera*	**−0.1**	−0.032
Teclea nobilis	0.043	−0.05	*Antidesma* sp	**−0.1**	−0.032
Croton megalocarpus	0.043	0.048	*Beilschmiedia ugandensis*	**−0.1**	−0.032
Chionanthus sp	0.032	−0.046	*Craibia brownii*	**−0.1**	−0.032
Kigelia moosa	0.032	−0.046	*Ficus natalensis*	**−0.1**	−0.032
Randia urcelliformis	0.031	−0.043	*Ficus ureolaris*	**−0.1**	−0.032
Allophylus abyssinica	0.019	0.045	*Harungana madaqascariensis*	**−0.1**	−0.032
Erythrina abyssinica sp *abyssinica*	0.019	0.045	*Lannea welwitschii*	**−0.1**	−0.032

Table 3 *Continued*

Species	PC 1	PC 2	Species	PC I	PC 2
Pancovia turbinata	0.019	0.045	*Macaranga schweinfurthii*	**−0.1**	−0.032
Phyllanthus discoideus	0.019	0.045	*Maerua duchesnei*	**−0.1**	−0.032
Pleiocarpa pycnantha	0.019	0.045	*Memecylon* sp	**−0.1**	−0.032
Xymalos monospora	0.019	0.045	*Morus lactea*	**−0.1**	−0.032
Albizia grandibracteata	0.008	−0.048	*Trichilia* sp2	**−0.1**	−0.032
Antiaris toxicaria	0.008	−0.048	*Trichilia splendida*	**−0.1**	−0.032
Casearia battisombei	0.008	−0.048	*Voacanga thouarsii*	**−0.1**	−0.032
Dovyalis macrocarpa	0.008	−0.048			

Table 4 Species that occurred at more than 4% of 90 sampling quadrats in sites of cluster A and cluster B paired by cluster analysis with a simple matching coefficient (SM) >0.9

Cluster A	Cluster B
Albizia glaberrima and *Allophylus abyssinica*	*Phyllanthus discoideus* and *Pancovia turbinata*
Harrisonia abyssinica and *Warburgia ugandensis*	*Symphonia globulifera* and *Aningeria altissima*
Bequaertiodendron oblanceolatum and *Cussonia holstii*	*Pleicarpa pycnantha* and *Newtonia buchananii*
Pleiocarpa pycnantha and *Ficus mucuso*	*Randia urcelliformis* and *Monodora myristica*
Polyscias fulva and *Milletia dura*	*Polyscias fulva* and *Ficus sansibarica*
Schrebera arborea and *Ficus exasperata*	*Balanites wilsoniana* and *Antiaris toxicaria*
Cordia millenii and *Balanites wilsoniana*	*Dictyandra arborescens* and *Craterispermum laurinum*
Craterispermum laurinum and *Bersama abyssinica*	*Dovyalis macrocarpa* and *Casearia battisombei*
Teclea nobilis and *Hallea rubrostipulata*	*Spathodea campanulata* and *Rubiaceae*
Strombosiopsis tetrandra and *Rubiaceae*	*Lovoa swynnertonii* and *Albizia grandibracteata*
Trema orientalis and *Bridelia micrantha*	*Morus lactea* and *Mitragyna rubrostipulata*
Randia urcelliformis Eggeling and *Dombeya mukole*	*Memecylon* sp and *Majidea fosteri*
Piptadeniatrum africanum and *Dasylepis eggelingii*	*Maerua duchesnei* and *Macaranga schweinfurthii*
Ehretia cymosa and *Bombax buonopozense*	*Lepidotrichilia volkensii* and *Lannea welwitschii*
Myrianthus arboreus and *Chionanthus mildbraedii*	*Harungana madaqascariensis* and *Harrisonia abyssinica*
Sapium ellipticum and *Majidea fosteri*	*Glyphaea brevis* and *Ficus ureolaris*
Lovoa sywnnertonii and *Leptonychia mildbaedii*	*Ficus natalensis* and *Ficus mucuso*
Celtis mildbraedii and *Baphiopsis parviflora*	*Ficus conraui* and *Erythrina abyssinica* ssp. *abyssinica*
	Elaeophorbia sp. and *Cynometra alexandri*
	Cussonia holsti and *Craibia brownii*
	Clausena anisata and *Chrysophyllum albidum*
	Chionanthus mildbraedii and *Celtis zenkeri*
	Celtis mildbraedii and *Bridelia micrantha*
	Bequaertiodendron oblanceolatum and *Bersama abyssinica*
	Baphiopsis parviflora and *Beilschmiedia ugandensis*
	Antidesma sp. and *Albizia gummifera*
	Trichilia sp1 and *Syzigium guineense*
	Strombosiopsis tetrandra and *Sapium ellipticum*
	Rauvolfia vomitaria and *Pterygota mildbraedii*
	Pseudospondias microcarpa and *Piptadeniastrum africanum*
	Vangueria apiculata and *Voacanga thouarsii*
	Trichilia sp2 and *Trichilia splendida*
	Zanthoxylum leprieurii and *Kigelia moosa*
	Warburgia ugandensis and *Croton megalocarpus*
	Ehretia cymosa and *Chionanthus* sp.
	Fagaropsis angolensis and *Albizia glaberrima*.

Table 5 Species associations' analysis of the tree species of Kanyawara K-15, Ngogo and Mainaro (cluster A) and of K-14 and K-30 (cluster B)

Cluster A1
Celtis durandii
Diospyros abyssinica
Markhamia lutea
Cluster A2
Aphania senegalensis
Baphiopsis parviflora
Celtis mildbraedii
Phyllanthus discoideus
Trilepisium madagascariensis
Uvariopsis congensis
Cluster A3
Aningeria altissima
Cassipourea ruwensorensis
Funtumia latifolia
Ilex mitis
Leptonychia mildbraedii
Lovoa swynnertonnii
Monodora myristica
Parinari excelsa
Premna angolensis
Pterygota mildbraedii
Strombosia scheffleri
Tabernaemontana pachysiphon
Cluster A4
Albizia glaberrima
Allophylus abyssinica
Balanites wilsoniana
Bequaertiodendron oblanceolatum
Bersama abyssinica
Blighia welwitschii
Bombax buonopozense
Bridelia micrantha
Celtis africana
Chaetachme aristata
Chionanthus mildbraedii
Chionanthus sp
Cordia millenii
Craterispermum laurinum
Croton megalocarpus
Cussonia holsti
Cynometra alexandri
Dasylepis eggelingii
Dictyandra arborescens
Dombeya mukole
Ehretia cymosa
Fagaropsis angolensis
Ficus exasperata
Ficus mukuso
Harrisonia abyssinica
Kigelia moosa
Majidea fosteri
Milletia dura
Mimusops bagshawei
Mitragyna rubrostipulata
Myrianthus arboreus
Neoboutonia melleri
Olea welwitschii
Piptadeniastrum africanum
Pleicarpa pycnantha
Polyscias fulva
Pseudospondias microcarpa
Randia urcelliformis
Rubiaceae
Sapium ellipticum
Schrebera arborea
Spathodea campanulata
Strombosiopsis tetrandra
Teclea nobilis
Trema orientalis
Warburgia ugandensis
Zanthoxylum leprieurii
Cluster B1
Trilepisium madagascariensis
Uvariopsis congensis
Cluster B2
Celtis durandii
Chaetachme aristata
Diospyros abyssinica
Dombeya mukole
Dovyalis macrocarpa
Funtumia latifolia
Markhamia lutea
Teclea nobilis
Cluster B3
Albizia grandibracteata
Aningeria altissima
Antiaris toxicaria
Aphania senegalensis
Balanites wilsoniana
Blighia welwitschii
Bombax buonopozense
Casearia battisombei
Cassipourea ruwensorensis
Celtis africana
Chrysophyllum gorungosanum
Cordia millenii
Craterispermum laurinum
Dictyandra arborescens
Erythrina abyssinica sp *abyssinica*
Ficus exasperate
Ficus sansibarica

Table 5 *Continued*

Ilex mitis
Leptonychia mildbraedii
Lovoa swynnertonnii
Milletia dura
Mimusops bagshawei
Monodora myristica
Morus lacteal
Myrianthus arboreus
Neoboutonia melleri
Newtonia buchananii
Olea welwitschii
Pancovia turbinata
Parinari excelsa
Phyllanthus discoideus
Pleicarpa pycnantha
Polyscias fulva
Polyscias fulva
Premna angolensis
Randia urcelliformis
Rubiaceae
Spathodea campanulata
Strombosia scheffleri
Strychnos mitis
Symphonia globulifera
Tabernaemontana pachysiphon
Tarenna pavetoides
Cluster B4
Alangium chinense
Albizia glaberrima
Albizia gummifera
Allophylus abyssinica
Antidesma sp
Baphiopsis parviflora
Beilschmiedia ugandensis
Bequaertiodendron oblanceolatum
Bersama abyssinica
Bridelia micrantha
Celtis mildbraedii
Celtis zenkeri
Chionanthus mildbraedii
Chionanthus sp
Chrysophyllum albidum
Clausena anisata
Coffea canephora
Craibia brownie
Croton megalocarpus
Cussonia holsti
Cynometra alexandri
Dasylepis eggelingii
Ehretia cymosa
Elaeophorbia sp
Erythrina excelsa

Table 5 *Continued*

Fagaropsis angolensis
Ficus conraui
Ficus mukuso
Ficus natalensis
Ficus ureolaris
Glyphaea brevis
Harrisonia abyssinica
Harungana madaqascariensis
Irvingia gabonensis
Kigelia moosa
Lannea welwitschii
Lepidotrichilia volkensii
Macaranga schweinfurthii
Majidea fosteri
Memecylon sp
MitragynarubrostipulataB4
Oncoba routledge
Piptadeniastrum africanum
Prunus africana
Pseudospondias microcarpa
Pterygota mildbraedii
Rauvolfia vomitaria
Sapium ellipticum
Schrebera arborea
Strombosiopsis tetrandra
Syzigium guineense
Trema orientalis
Trichilia sp1
Trichilia sp2
Trichilia splendida
Vangueria apiculata
Voacanga thouarsii
Warburgia ugandensis
Xymalos monospora
Zanthoxylum leprieurii

Species assemblages (A1–A4) and (B1–B4) were defined using a simple matching coefficient of 0.0.

logging than the sites in cluster A. The species descriptive of cluster B (Table 3) are characteristic of undisturbed areas in Kibale forest representing climax forest tree communities (Kasenene, pers. comm.).

However, these results do not preclude the fact that both abiotic and biotic factors are important in characterizing tree species assemblages in sites. Due to a paucity of data on several important factors, we can only speculate as to the other potential sources of these differences in floristic composition between sites other than the differences in logging history. They include small variations in rainfall in different sites, soil composition, elevation, temperature and

historical differences in the distribution and abundance of large mammals (Struhsaker, Lwanga & Kasenene, 1996; Chapman *et al.*, 1997). Primates and ungulates are known to influence the floristic composition of tropical forests via their roles as seed dispersers (Nchanji & Plumptre, 2003).

Species distribution

Many tree species had widespread distributions including *Aningeria altissima, Aphania senegalensis, Blighia welwitschii, Celtis africana, Celtis durandii, Chaetachme aristata, Diospyros abyssinica, Dombeya mukole, Fagaropsis angolensis, Funtumia latifolia, Markhamia lutea, Monodora myristica, Premna angolensis, Prunus africana, Trema orientalis, Trilepisium madagascariensis* and *U. congensis.* These were recorded in all the five sampled sites. The most abundant species however, included *C. durandii, D. abyssinica, M. lutea, F. latifolia* and *U. congensis*. These were recorded in at least 48% of the plots sampled. Species whose distributions were either mostly or entirely restricted to one compartment or site included *C. mildbraedii, Chrysophyllum albidum, Cussonia holsti, Cynometra alexandri, Elaeophorbia* sp., *Erythrina excelsa, Ficus conraui, Ficus mukuso, Glyphaea brevis, H. abyssinica, Lepidotrichilia volkensii, Majidea fosteri, Pterygota mildbraedii, Rauvolfia vomitaria, Sapium ellipticum, Strombosiopsis tetrandra, Syzigium guineense, Tarenna pavetoides, Trichilia* sp1 and *Vangueria apiculata.* The least common species included *Coffea canephora*, *Irvingia gabonensis*, *Oncoba routledge*, *P. africana*, *Xymalos monospora* and *Alangium chinense*. These were recorded in less or equal to 4% of the sampled quadrats.

In conclusion, it is evident that Kanyawara K-30, K-14, K-15 and Ngogo forests found in the north and central part of Kibale National Park, represent a mixed forest largely influenced by varying logging intensities in the past. The climax forest is in the southern part of the park where Mainaro site is located. Within each forest type, there were different species associations and these appear to be a reflection of the species that have regularly occurred together in these sites. Further investigation is required to include other forest parts not considered in this study.

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References

Brugiere, D., Gautier, J.-P., Moungazi, A. & Gautier-Hion, A. (2002) Primate diet and biomass in relation to vegetation composition and fruiting phenology in a rain forest in Gabon. *Int. J. Primatol.* **23**, 999–1024.

Butynski, T.M. (1990) Comparative ecology of blue monkeys (*Cercopithecus initis*) in high- and low-density subpopulations. *Ecol. Monogr.* **60**, 1–26.

Cannon, C.H., Peart, D.R. & Leighton, M. (1998) Tree species diversity in commercially logged Borneon rainforest. *Science* **28**, 1366–1368.

Chapman, C.A. & Chapman, L.J. (1997) Forest Regeneration in logged and unlogged Forests of Kibale National Park, Uganda. *Biotropica* **29**, 396–412.

Chapman, C.A., Chapman, L.J., Wrangham, R., Isabirye-Basuta, G. & Ben-David, K. (1997) Spatial and temporal variability in the structure of a tropical forest. *Afr. J. Ecol.* **35**, 287–302.

Davies, A.G. (1994) Colobine populations. In: *Colobine Monkeys: Their Ecology, Behaviour and Evolution* (Eds A. C. Davies and J. F. Oates). Cambridge University Press, Cambridge.

Eilu, G., Hafashimana, D. & Kasenene, J.M. (2004) Density and speciesdiversity of trees in four tropical forests of the Albertine rift, Western Uganda. *Biodivers. Res.* **10**, 303–312.

Gauch, H.G. (1982) *Multivariate Analyses in Community Ecology*. Cambridge University Press, Cambridge, England.

Ghigleiri, M.P. (1984) *The Chimpanzees of Kibale Forest: A field study of Ecology and social structure*, 1st edn. Columbia University Press, New York.

Hart, J.A. (2001) Diversity and abundance in an African forest ungulate community and implications for conservation. In: *African Rain Forest Ecology and Conservation* (Eds W. Weber, L. J. T. Whim, A. Vedder and L. Naughton-Treves). Yale University Press, New Haven.

Howard, P.C. (1991) *Nature Conservation in Uganda's tropical forest reserve*. IUCN publication, Switzerland.

Howard, P.C. & Davenport, T.R.B. (1996) *Forest Biodiversity Reports*, Vol. **1–33**. Uganda Forest Department, Kampala.

Jongman, R.H.G., Ter Braak, C.J.F. & Van Tongeren, O.F.R. (1995) *Data Analysis in Community and Landscape Ecology*. Cambridge University Press, Cambridge.

Kasenene, J.M. (1987) *The influence of mechanical selective logging, felling intensity and gap size in the regeneration of a tropical moist forest in the Kibale Forest Reserve*. Ph.D Dissertation, Michigan State University, Uganda.

Kent, M. & Coker, P. (1992) *Vegetation description and analysis: a practical approach*. John Wiley & Sons, Chichester, England.

Kovach, W.I. (1999) *A Multivariate Statistical Package for Windows, Version 3.1*. Kovach computing services, Pentraeth, Wales.

Ludwig, J.A. & Reynolds, J.F. (1988) *Statistical Ecology: A Primer on Methods and Computing*. John Wiley and Sons, New York.

Mentis, M.T. (1983) Towards objective veld condition assessment. *Proc. Grassl. Soc. South. Afr.* **18**, 77–80.

NCHANJI, A.C. & PLUMPTRE, A.J. (2003) Seed germination and early seedling establishment of some elephant-dispersed species in Banyang-Mbo Wildlife Sanctuary, south-western Cameroon. *J. Trop. Ecol.* **19**, 229–237.

ØKLAND, R.H. (1990) Vegetation ecology: theory, methods and applications with reference to Fennoscandia. *Sommerfeltia* **1**, 4–233.

OSMASTON, H.A. (1959) *Working plan for Kibale & Itwara forests*. Uganda Forestry department, Entebbe.

PARTHASARATHY, N. (1999) Tree diversity and distribution in undisturbed and human-impacted sites of tropical wet evergreen forest in southern Western Chats, India. *Biodivers. Conserv.* **8**, 1365–1381.

PHILLIPS, O.L., HALL, P., GENTRY, A.H., SAWYER, S.A. & VASQUEZ, R. (1994) Dynamics and species richness of tropical rain forests. *Proc. Natl Acad. Sci. U.S.A.* **91**, 2805–2809.

PIELOU, E.C. (1984) *Interpretation of Ecological Data*. John Wiley and Sons, New York.

POLHILL, R.M., MILNE-REDHEAD, E., TURRILL, W.B. & HUBBARD, C.E. (1952) *Flora of Tropical East Africa (in many parts)*. Crown Agents, London and Balkema, Rotterdam.

PROCTOR, J., ANDERSON, J.M., CHAI, P. & VALLACK, H.W. (1983) Ecological studies in four contrasting lowland rain forest types in Gunung Mulu National Park, Sarawak. I. Forest environment, structure and floristics. *J. Ecol.* **71**, 237–260.

SHEIL, D., SAYER, J.A. & OBRIEN, T. (1999) Tree species diversity in logged tropical rainforests. *Sciencemag* **284**, 5420.

SKORUPA, J.P. & KASENENE, J.M. (1984) Tropical forest management: can rates of natural tree falls help guide us? *Oryx* **18**, 96–101.

SKORUPA, J.P. (1988) *The effects of selective timber harvesting on rain - forest primates in Kibale Forest*. PhD. Thesis, University of California Davis, Uganda.

STRUHSAKER, T.T. (1997) *Ecology of an African Rain Forest; Logging in Kibale and the Conflict between Conservation and Exploitation*. University of Florida, Gainesville.

STRUHSAKER, T.T., LWANGA, J. S. & KASENENE, J.M. (1996) Elephants, selective logging and forest regeneration in the Kibale Forest, Uganda. *J. Trop. Ecol.* **12**, 45–64.

SWAMY, P.S., SUNDARAPANDIAN, S.M., CHANDRASEKAR, P. & CHANDRASEKARAN, S. (2000) Plant species diversity and tree population structure of a humid tropical forest in Tamil Nadu, India. *Biodivers. Conserv.* **9**, 1643–1669.

TER STEEGE, H., SABATIER, D., CASTELLANOS, H., VAN ANDEL, T., DUIVENVOORDEN, J., DE OLIVEIRA, A.A., EK, R., LILWAH, R., MAAS, P. & MORI, S. (2000) An analysis of the floristic composition and diversity of Amazonian forests including those of the Guiana Shield. *J. Trop. Ecol.* **16**, 801–828.

VAN ORSDOL, K.G. (1983) *The status of Kibale Forest Reserve of Western Uganda and recommendations for its conservation and management*. Report to the New York Zoological Society, Bronx, New York.

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